

THE *SALSOLA TRAGUS* COMPLEX IN CALIFORNIA (CHENOPODIACEAE):  
CHARACTERIZATION AND STATUS OF *SALSOLA AUSTRALIS* AND THE  
AUTOCHTHONOUS ALLOPOLYPLOID *SALSOLA RYANII* SP. NOV.

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ABSTRACT

Over the past century in California, the invasive weed *Salsola tragus* (russianthistle) has become a widespread and troublesome pest plant. Early attempts at biological control of russianthistle achieved only partial success. Efforts to improve effectiveness of renewed biocontrol efforts revealed that two distinct, often sympatric, genetic entities comprise what has been called *Salsola tragus*: *Salsola tragus* and *Salsola* 'type B'. Efforts to identify and characterize 'type B' resulted in recognition of a third form, 'type C'. We present a taxonomic and morphological examination of *Salsola tragus*, *Salsola* 'type B', *Salsola* 'type C' and *Salsola paulsenii* using discriminant analysis with DNA sequence genotypes as the taxonomic framework. *Salsola tragus* and 'type B' were morphologically distinct; 'type C' was morphologically intermediate between them and contained DNA sequence genotypes that were an additive mixture of haplotypes mostly exclusive to tetraploid *S. tragus* and others exclusive to diploid 'type B'. 'Type C' is a fertile allohexaploid that originated via hybridization between *S. tragus* and 'type B'. We provide a pre-existing name, *Salsola australis*, for 'type B', and propose *Salsola ryanii* sp. nov. for 'type C'. Morphological variation, habitats, and dispersal behaviors among these *Salsola* taxa were examined in the herbarium and in the field. These are compared and discussed.

Key Words: Chenopodiaceae, discriminant, PEPC, polyploidy, russianthistle, *Salsola*, speciation, tumbleweed.

Open almost any floristic account that includes California, and the non-native plant known by the common name russianthistle or tumbleweed is referred to by one of several different scientific names. In 1996, S. L. Mosyakin showed that *Salsola tragus* L. was the correct name to use for the widespread North American tumbleweed. Thus, at least the following six names should be considered synonyms of or misapplications to *Salsola tragus* L.: *Salsola australis* R. Br., *S. iberica* (Sennen & Pau) Botsch., *S. kali* L. subsp. *ruthenica* (Iljin in Keller et al.) Soó & Jav. in Soó et Javorka, *S. kali* L. var. *tenuifolia* Tausch ex Moq., *S. pestifer* A. Nelson (*S. 'pestifera'*), and *S. ruthenica* Iljin in Keller et al. Some of these may be actual synonyms of *S. tragus* and others distinct or segregate taxa, but their application to genuine *Salsola tragus* is, as presently understood, uncertain or incorrect. And so despite the considerable variation within and among populations of *S. tragus* in North America, all were previously referenced in whole by any one of the six names above, or by *S. tragus* itself. *Salsola tragus sensu lato* will here be used in reference to this morphologically variable group of plants. In North America, *S. tragus sensu lato* appeared

first in the mid-19<sup>th</sup> century (Ryan and Ayres 2000); in California it arrived around 1890 in the Mojave Desert near Lancaster in San Bernardino Co., and had been collected widely by 1911 (Jepson 1914).

In California and Arizona, *Salsola tragus sensu lato* is distributed at elevations below about 2500 m where it grows in semi-alkaline, open, and usually disturbed habitats. In California, it occurs along the south coast, in the mountain foothills, the low and high deserts and the Central Valley; it is also on the Modoc Plateau, throughout the eastern Sierra Nevada valleys, and in the Mojave Desert. The largest California populations occur from the southern Sacramento Valley south to Tehachapi Pass, with extensive stands in the northern San Joaquin Valley. There is considerable among-year variation and large stands frequently appear in the Mojave Desert and California South Coast Ranges. Other than as a casual, it is absent only from the mesic North Coast Ranges, the high Sierra Nevada and the Cascade Mountains.

Wherever stands occur, tumbling plant 'skeletons' in the late fall and winter pile against intercepting fences, fill drains and ditches and are

a moving hazard on roads. Biological control efforts in the 1960's resulted in the introduction of two Coleophorid moths (*Coleophora klimeschiella* Toll and *Coleophora parthenica* Meyrick), but these failed to significantly reduce plant abundance (Goeden and Pemberton 1995). During a second biocontrol research effort in the late 1990's, field observations suggested that russianthistle populations expressed differential susceptibility to herbivory or infection. Bruckart et al. (2004) found differential establishment of the fungi *Colletotrichum gloeosporioides* (Penz.) Penz. and *Uromyces salsolae* Reich. among local populations of russianthistle and similar differential establishment of insect biocontrol agents was documented by Sobhian et al. (2003).

With these biocontrol inconsistencies in mind, Ryan and Ayres (2000) examined allozyme variation within California russianthistle and found that two distinct genetic forms were sometimes present within populations that were otherwise thought to be monotypic. Although both forms had the outward appearance of the common tumbleweed, experienced observers found they were more or less visually distinguishable. Moreover, a chromosome count showed that one was diploid ( $2n = 18$ ), the other tetraploid ( $2n = 36$ ) (Ryan and Ayres 2000).

Subsequently, a qualitative assessment by the first author revealed that the tetraploid formed rounded, ascending-branched tumbleweeds with a dense spicate inflorescence and wingless mature tepals at the lower nodes. The diploid in contrast, had a more upright habit, was more horizontally branched, had less condensed inflorescences, and mature fruits with winged tepals at both the upper and lower nodes. At the time, it was not known which type, if either, was nomenclaturally typical *Salsola tragus*, and the tetraploid was arbitrarily referred to as 'type A', the diploid as 'type B' (Ryan and Ayres 2000). Mosyakin concluded, based on his familiarity with the *S. tragus* lectotype, that the tetraploid 'type A' was the typical form (S. L. Mosyakin, Kholodny Institute of Botany, Kiev, Ukraine, personal communication), and several years later, Gaskin et al. (2006) confirmed that application using molecular markers.

The indigenous range of 'type A' (*Salsola tragus* sensu stricto) was therefore known (Mosyakin 1996; Rilke 1999). However, plants referable to 'type B' were not described by Mosyakin (1996, 2003), and Rilke (1999) discussed them only as a minor variant of *S. tragus*, adventive in southern Africa and possibly Australia. In contrast, a cluster analysis of RAPDs data for *Salsola tragus* sensu lato, grouped 'type B' not with 'type A', but with *Salsola paulsenii* Litv. (Ryan and Ayres 2000).

During Ryan and Ayres' examination of *Salsola tragus*, a third allozyme profile in

California *Salsola* was recognized (F. Ryan USDA Agricultural Research Service, Fresno, CA personal communication). The tested material, from near Coalinga in Fresno County, was given the working title 'type C'.

Gaskin et al. (2006) identified a series of nuclear DNA sequence haplotypes that distinguished *Salsola* 'type A' and 'type B'. Here we provide a morphologic and taxonomic examination of *Salsola tragus*, 'type B', and 'type C' based on the differential presence of those haplotypes, with a morphologic-only examination of *Salsola paulsenii* for context. We discuss these plants' variation, and provide names for 'type B' and 'type C'. We conclude with discussion of their observed ecological behaviors and comment on adaptation in 'type C'.

## METHODS

### Molecular

Following extraction of DNA by standard methods (as described in Ryan and Ayres 2000), amplification of the intron between the fourth and fifth exon of the phosphoenolpyruvate carboxylase gene utilized the primer pair ppcx4f (5'-ACTCCACAGGATGAGATGAG-3') and ppcx5r (5'-GCAGCCATCATTCTAGCCAA-3') designed by J. F. Gaskin from the sequences of other taxa of the Caryophyllales found in GenBank. Amplification was conducted after a 2 min denaturation at 95°C and consisted of 30 cycles of 95°C (1 min), 52°C (1 min) and 72°C (2 min); followed by 5 min at 32°C. The two PCR products (one band approximately 500 bases in length and the other approximately 400 bases in length) were present in all samples. These bands were separated by electrophoresis on a 2% agarose gel and the shorter band was excised (the identity of the longer band is unknown, and its sequence variation was not useful for this analysis). DNA was purified with the QIAquick Gel Extraction Kit (Qiagen Inc., Valencia, CA). The resultant template was sequenced on a Beckman CEQ 2000XL (Beckman Coulter Inc., Fullerton, CA) using reagents and protocols supplied by the manufacturer and the same primers mentioned above. Each heterozygotic genotype was cloned and sequenced to determine the haplotypes involved. Clones were created using the Promega pGEM-T Vector System II (Promega Corp., Madison, WI), then sequenced using the protocol above. Sequences were aligned by hand using SE-AL software (Rambaut 1996) and are available in GenBank (accession numbers are in Gaskin et al. 2006). Haplotypes were arranged manually into a most parsimonious network (Fig. 1; also see Gaskin et al. 2006, Fig. 2).

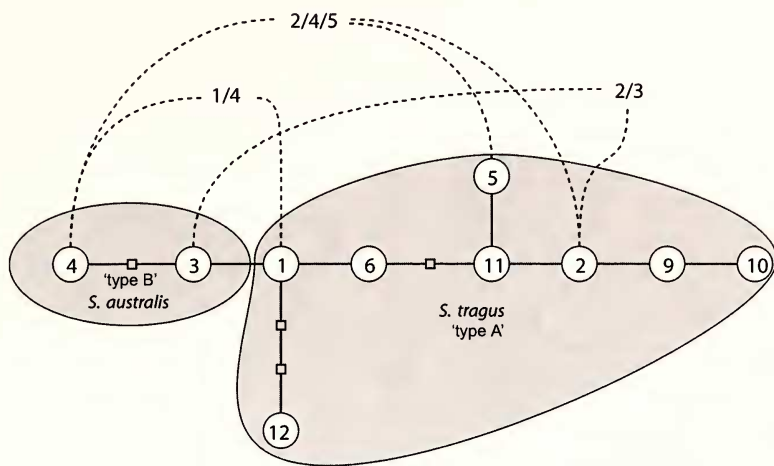


FIG. 1. Haplotype network of DNA sequences of the fourth intron of the PEPC gene region for 86 samples of *Salsola* species from the USA, Africa, and Eurasia (see Gaskin et al. 2006). Circles represent haplotypes recovered, and squares along lineages in between circles indicate haplotypes not recovered. Each link between haplotypes indicates one mutational event. Angle of bifurcation and length of link between haplotypes have no significance. The loops that surround portions of the haplotype network indicate taxonomic status of plant collections sampled. Dotted lines indicate which haplotypes were combined to form 'type C' genotypes 1/4, 2/3, and 2/4/5, shown at top of figure.

### Nomenclature

*Salsola tragus* is also polymorphic in its native Eurasia where it has more than 60 names associated with it. The taxonomic synopsis by Rilke (1999) was used to indicate names that could be applicable to 'type B', and *S. L. Mosyakin* suggested others. Many of these nomenclatural types were examined by Dr. Mosyakin at the V. L. Komarov Botanical Institute in St. Petersburg, Russia (LE); he also provided digital images of specimens whose winged fruits appeared similar to those of 'type B'.

The types examined at LE were *S. centralasiatica* Iljin, *S. aptera* Iljin, *S. gobicola* Iljin, *S. microkali* M. Popov, *S. kali* var. *splendens* Litv., *S. pellucida* Litv. (a *nomen nudum*), *S. praecox* (Litv.) Iljin, and *S. paulsenii* Litv. subsp. *oreophila* Kinz. An isotype of *Salsola australis* from the British Museum (BM) was examined at the California Dept. of Food and Agriculture Herbarium (CDA). The holotype of *Salsola kali* L. subsp. *austroafricana* Aellen at Botanische Staatssammlung München (M) was viewed as a high-resolution digital image. Dr. Lincoln Smith and M. I. Wibawa of the USDA Biocontrol Laboratory in Albany, CA, imaged specimens at Université Montpellier, France (MPU) and the Royal Botanical Gardens, Kew, England (K) respectively. Descriptions and discussion in various North American, European, Asian, African and Australian floras were also consulted.

### Morphology: Experimental Materials and Analysis

Once a search image was established, *Salsola tragus* 'type A' and *Salsola* 'type B' were readily

separable in the field. However, their observed tendency to grow in slightly different environments allowed the possibility that plastic responses to environment could influence their appearance. Their reaction to a common environment was tested in a garden of thirty-two adjacent plots established in Sacramento, CA. The test plants were grown from seed that had provenances in the San Joaquin Valley and Mojave Desert (Appendix I).

Additional *Salsola* specimens were collected in the wild specifically for this study and were combined with existing herbarium specimens at CDA to both provide variants for comparison and to supplement the common garden material. To establish circumscription of the primary (*S. tragus* 'type A', 'type B' and *S. paulsenii*) group compositions, 181 specimens were examined and their morphologic features measured. Of these, 112 were from the common garden, 56 were collected specifically for this study, and 13 were from the CDA herbarium. Among these were 26 specimens with known haplotype sequences (genotypes), comprised of six *Salsola tragus*, seven 'type B' and 13 'type C'. These latter were used to establish the correlation between genotype and morphologic group identity. Discriminant functions separating the "core" three groups, *S. tragus* ('type A'), *S. australis* ('type B'), and *S. paulsenii*, were generated for one dataset; a second set of functions were generated to separate the above 'core' three, plus a sample of 'type C' individuals with confirmed genotypes. An additional set of 25 specimens with known genotypes was used to test the functions' utility. This group of specimens included 11 plants with *Salsola tragus* genotypes, eight 'type B' and six

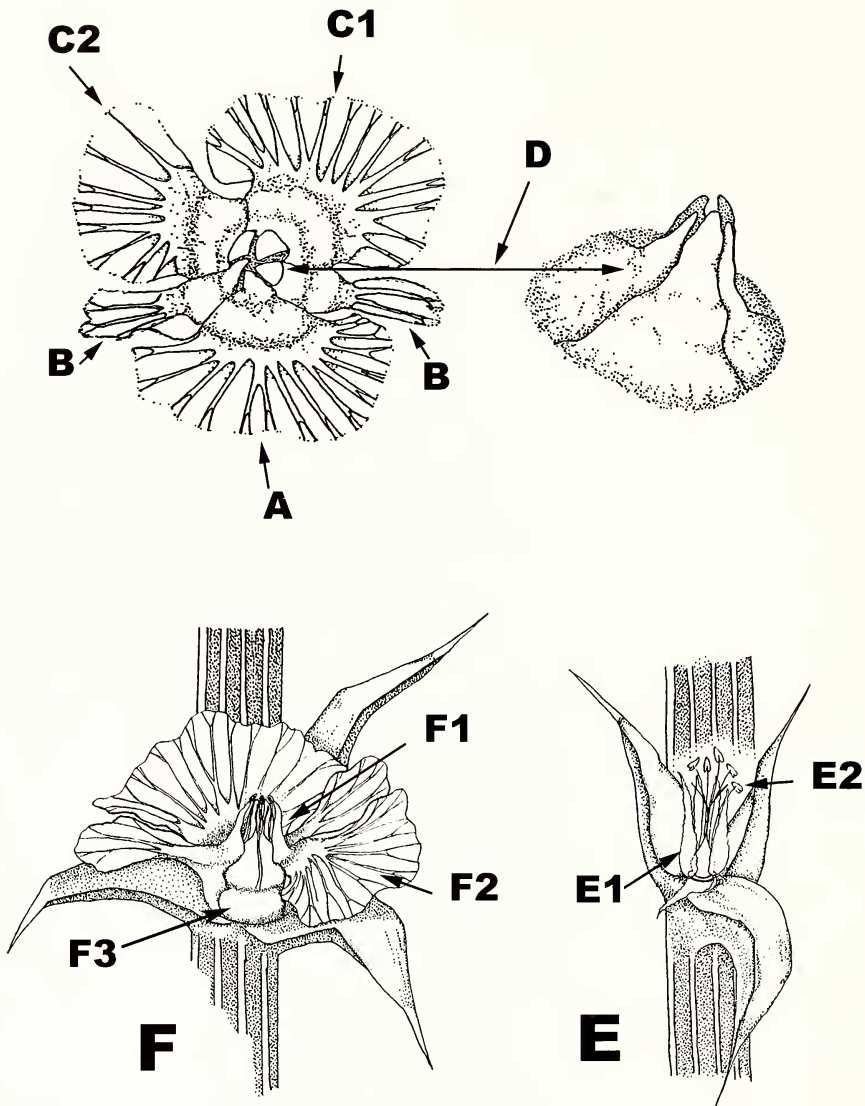


FIG. 2. *Salsola* sect. *Kali* flowers and fruits. TOP: *S. tragus*: Front view of mature flower with fully developed tepal wings. A, major tepal wing; B, minor tepal wings; C1, median tepal wing with consistent shape; C2, median tepal wing with inconsistent shape; D, mature tepals front & top front view. BOTTOM: *Salsola* 'Type B': E, side view of flower at anthesis, front tepal removed for display; E1, tepal segment; E2, stamens; F, side view of flower in fruit with front winged tepals removed for display; F1, tepals in fruit; F2, fully developed tepal wing.

'type C'. Among these was one morphologically unusual 'type B', several plants with *S. tragus* genotypes that, by inspection alone, appeared to be 'type C' plus a single South African and one Australian specimen (Table 1; Appendix III). Collection data for all the specimens examined are given in Appendices I and III.

Dried plant material was softened in Pohl's solution for examination and dissection. Data were taken with an ocular micrometer to the closest 0.1 mm or 0.05 mm depending upon the necessary magnification. For discrimination raw data were converted to a range of 0-1 using Gower's algorithm (Sneath and Sokal 1973). All

analyses were performed in SAS Systems JMP 5.1.

#### Morphometric Characters

For each available and quantifiable morphologic feature, a measurement standard was established, a subsample measured, and the results compared among the three base groups, *Salsola tragus*, 'type B' and *S. paulsenii*. Bi-modal or tri-modal patterns could indicate a discrimination capacity and raw data were taken for these characters.

At fruit maturation, tepals in *Salsola* sect. *Kali* Dumont develop wings on the abaxial surface.

TABLE 1. SPECIMENS USED TO TEST THE DISCRIMINATION FUNCTION'S MORPHOLOGICAL CLASSIFICATION OF KNOWN GENOTYPES. All were of known genotype, and were not used to calculate the actual functions. Vouchers are at CDA unless specified otherwise. Specimens in bold discriminated morphologically outside their genotype (see Fig. 7). Collection details in Appendix III. CG = "common garden". \*Single known polyploid with only *Salsola tragus* haplotypes.

Specimen	County/ Country	Genotype	Plant DNA #	PEPC Genotype Assignment	Discriminant Classification
C. Borger 01 (PERTH)	New South Wales, Australia	3/3	7652	'type B'	'type B'
<b>Moran 21152</b>	<b>Baja California, Mexico</b>	<b>1/2</b>	<b>6132</b>	<b><i>S. tragus</i></b>	<b>'type C'</b>
Ahart 8295	Butte, CA	1/2	6134	<i>S. tragus</i>	<i>S. tragus</i>
Akers RT-014-1	Fresno, CA	2/5	4133 (Gaskin et al. 2006)	<i>S. tragus</i>	<i>S. tragus</i>
CG A-10/1	Fresno, CA	1/4	6117	'type C'	'type C'
CG A-10/4	Fresno, CA	1/4	6120	'type C'	'type C'
CG B-3/2	Fresno, CA	1/4	6122	'type C'	'type C'
CG C-2/1	Fresno, CA	1/4	6125	'type C'	'type C'
Akers RT-055-1	Kern, CA	2/5/4	6106	'type C'	'type C'
<b>Akers RT-056-1</b>	<b>Kern, CA</b>	<b>2/5</b>	<b>6107</b>	<b><i>S. tragus</i></b>	<b>'type C'</b>
<b>Akers RT-065-1</b>	<b>Kern, CA</b>	<b>1/2/5*</b>	<b>6110</b>	<b><i>S. tragus</i></b>	<b>'type C'</b>
Akers RT-069-2	Kern, CA	2/5/4	6111	'type C'	'type C'
Akers RT-074-1	Kern	3/3	4142 (Gaskin et al. 2006)	'type B'	<i>S. australis</i>
CG A-7/2	Fresno, CA	1/2	6129	<i>S. tragus</i>	<i>S. tragus</i>
CG A-7/3	Fresno, CA	1/2	6130	<i>S. tragus</i>	<i>S. tragus</i>
CG A-7/4	Fresno, CA	1/2	6131	<i>S. tragus</i>	<i>S. tragus</i>
<b>Hrusa 16172</b>	<b>Kern, CA</b>	<b>3/3</b>	<b>6140</b>	<b>'type B'</b>	<b>'type C'</b>
Villegas B247-1	Los Angeles, CA	4/4	6168 (Gaskin et al. 2006)	'type B'	'type B'
Villegas B247-2	Los Angeles, CA	4/4	6169 (Gaskin et al. 2006)	'type B'	'type B'
Akers RT-013-1	Merced, CA	4/4	4140 (Gaskin et al. 2006)	'type B'	'type B'
Akers RT-030-2	Merced, CA	4/4	4141 (Gaskin et al. 2006)	'type B'	'type B'
Akers RT-005-3	Solano, CA	1/2	4135 (Gaskin et al. 2006)	<i>S. tragus</i>	<i>S. tragus</i>
Rejmanek SA#1	South Africa	3/3	6798	'type B'	'type B'
<b>Akers RT-042-1</b>	<b>Stanislaus, CA</b>	<b>2/5</b>	<b>4136 (Gaskin et al. 2006)</b>	<b><i>S. tragus</i></b>	<b>'type C'</b>
<b>Akers RT-042-3</b>	<b>Stanislaus, CA</b>	<b>1/2</b>	<b>4137 (Gaskin et al. 2006)</b>	<b><i>S. tragus</i></b>	<b>'type C'</b>

Wing development varies among the species, but the California taxa have five wings, one on each tepal. We observed that, within an individual, their form was generally consistent. Alone or in combination with other features, Rilke (1999) also found tepal-wing characters useful in *Salsola* sect *Kali*. The basic pattern is of one large or major wing bordered by two small or minor wings, with each of these adjacent to one of two middle or median wings (Fig. 2). One of the median wings exhibited considerable intra-individual shape variation, as less often did one of the minor wings. We measured only the more developmentally consistent of the two median and minor wings. Because of their stability, availability, and ease of quantification, tepal-wing features dominated the morphometric data.

Length of the mature anther sac was the only quantifiable non-tepal feature identified. Species of *Salsola* sect. *Kali* produce flowers over a considerable period and all but the latest season and immature specimens had mature anthers available. Anther sac length was also utilized by Rilke (1999) and it appears to be a useful taxonomic characteristic in the section. We used only fully mature dehisced anther sacs; those mummified or partially developed were excluded.

These fruit and anther characteristics were utilized as both direct measurements and as ratios derived from them (Table 2).

## RESULTS AND DISCUSSION

### Variation among PEPC Intron Sequences

Our sampling of 'type B' beyond those specimens listed in Gaskin et al. (2006) found no previously unreported haplotypes. In summary, two haplotypes (3 and 4) are known from 'type B', neither of which occur in *Salsola tragus* ('type A'), or in *Salsola paulsenii*. Gaskin et al. (2006) reported a specimen of 'type B' from the Phoenix, AZ, vicinity with the heterozygote genotype 3/4; all other individuals sequenced were homozygous for haplotype 3 or haplotype 4. The sampled distribution of these two haplotypes in California and Arizona is shown in Fig. 3A–B. The 'type B' genotypes in far southern Arizona, Texas and (probably) elsewhere in North America are not yet known.

The domination of the 'type B' dataset by homozygote genotypes suggests that some form of autogamy or agamospermy may occur in these plants. Our close observation of flowers during

TABLE 2. CHARACTERS USED IN THE MORPHOMETRIC ANALYSIS. Those with an asterisk preceding were, in combination, usefully diagnostic of *Salsola* types 'A', 'B', 'C' and *S. paulsenii*. Major wing width was tightly correlated with winged fruit diameter, but these in combination improved discrimination.

Taxonomic value	Character
1. Discriminant	*Winged-fruit diameter
2. Non-systematic	Major-wing length
3. Discriminant	*Major-wing width
4. Non-systematic	Major-wing length to width ratio
5. Non-systematic	Minor-wing length
6. Discriminant	*Minor-wing width
7. Non-systematic	Minor-wing length to width ratio
8. Non-systematic	Median-wing length
9. Non-systematic	Median-wing width
10. Non-systematic	Median-wing length to width ratio
11. Discriminant	*Anther length
12. Non-systematic	Ratio of minor-wing width to major-wing length

morphometric examination showed that pre-dehiscent anthers are already exerted, and cleistogamous flowers do not appear present. Self-fertilization behavior would be then at least partially geitonogamous and not restrictive of potential out-crossing. Asexual seed formation could help explain both the dominance of homozygotes in 'type B' and how the majority of 'type A' genotypes are two recurring heterozygote combinations, 1/2 and 2/5 (Gaskin et al. 2006). However, this is speculative as *Salsola* breeding behavior and its influence on the genetic and morphological variation patterns is not currently understood.

Most of the original PEPC sequences (haplotypes) generated for this study were from those plants called 'type C'. The genotypes recovered from most of these specimens were mixed combinations of *Salsola tragus* and 'type B' haplotypes (Table 1; Appendices II and III), although several similar-appearing plants had only *S. tragus* haplotypes. Among the five haplotypes recorded for 'type C', haplotype 1 is characteristic of *Salsola tragus sensu stricto* and occurs in *Salsola paulsenii*; haplotypes 2 and 5 are known from *S. tragus sensu stricto* only, and haplotypes 3 and 4 are restricted to 'type B' (Gaskin et al. 2006). These were combined among individuals of 'type C' to form three different genotypes (Fig. 1). The original 'type C' common garden offspring, from Coalinga (Fresno Co., CA), contained a combination of haplotypes 1 and 4. Haplotype 1 is found in both *Salsola paulsenii* and *Salsola tragus*, but there was nothing in the morphology of these specimens to suggest *Salsola paulsenii* was involved in the parentage. Plants from Yuba City and near Daugherty in Sutter Co. CA, were a mix of *Salsola tragus* haplotype 2 and 'type B' haplotype 3. A third mixture from about Maricopa in Kern

Co., CA, contained three haplotypes, 2 and 5 from *Salsola tragus* and haplotype 4 from 'type B'.

### Morphometric Variation

Both seasonal and non-seasonal developmental variation precluded the quantification of numerous morphologic features; others were not all available on single specimens. Features not readily usable or available included bract connation, growth habit, trichome type, including position and occurrence patterns, shape features of the leaves, bracts and spines, plus the seed shape features listed in Ryan and Ayres (2000). While some of these, particularly trichome type, proved useful qualitative taxonomic characters (Table 3), they were not included in the quantitative data matrix.

Living plants in the common garden were readily recognized as 'type B', *S. paulsenii* or *S. tragus*, and after drying, the cultivated specimens were not distinguishable from comparable wild-collected material. Environment appears not to be a significant influence on morphological response in *Salsola* sect. *Kali*, and therefore the morphometric analyses reported here combined the wild and common garden datasets. We found that a combination of three characters, anther sac length, minor tepal-wing width, and overall winged-fruit diameter (Table 2), in two functions, could accurately classify all 183 specimens representing this three-group 'core' (Fig. 4).

The first discriminant function separated *Salsola tragus* and 'type B' by the broad minor wing and short anthers in the latter that contrasted with the narrow minor wing and longer anthers of *S. tragus*. The second function separated *S. tragus* from *S. paulsenii* due to the broad overall winged fruit diameter and short anthers in the latter. Thirteen 'type C' individuals (Appendix II) were then added to the three-group "core" dataset and new functions calculated. Discrimination accuracy was reduced to 97.8% (4 misclassifications out of 196). A discriminant score plot showed that the 'type C' specimens were interpolated between *S. tragus* and 'type B' (Fig. 5), due to their intermediate-width minor wings and mid-length anther sacs. The four misclassifications were three specimens previously classifying as *S. tragus* ('type A') that now classified as 'type C', and one a known 'type C' that re-classified as *S. tragus*. The stepwise addition of a fourth potential discriminator, the major tepal-wing width, regained 100% accurate classification. Although the major tepal-wing width and the overall winged-fruit diameter were correlated overall ( $r^2 = 0.90$ ), the correlations were different among the four groups. Relative to the overall winged-fruit diameter, the major wing is broad in *S. tragus* and *S. paulsenii*, while it is

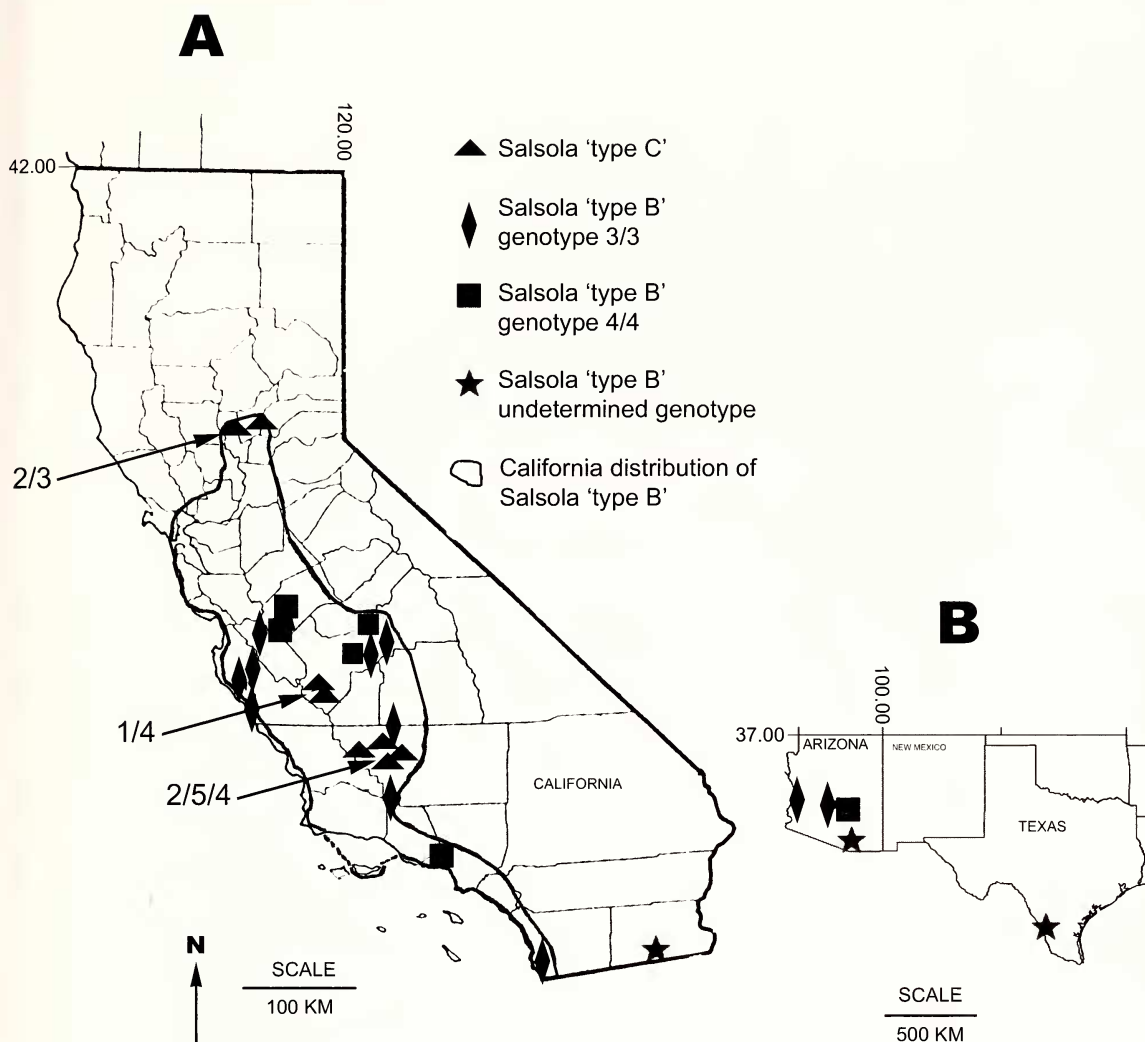


FIG. 3. Distribution of *Salsola* 'type B' and *Salsola* 'type C' in California and the US southwest. California specimens of known genotype are individually plotted. Arrows indicate the single known genotype for each population of 'type C'. The dark line surrounds the known distribution of 'type B'. *Salsola tragus* occurs throughout California; only along the immediate coast, the high Sierra and in the Klamath/Siskiyou regions is it rarely encountered. Outside of the outlined region *Salsola* 'type B' distribution is imperfectly known.

narrower in 'type B' and 'type C' (compare Figs. 6C and 6D; also Fig. 8).

After completion of the above analyses, the 25 individuals of known genotype but not used for the function calculations, were scored for the above four discriminating characters. Their discriminant scores are plotted in Fig. 7 and the specimens are listed in Table 1 and Appendix III.

Among these, five *S. tragus* and one 'type B' misclassified as 'type C'. Among those with *S. tragus* genotypes, Moran 21152 from Baja California had most of the features and the habit of *Salsola tragus sensu stricto* (see Table 3) but had unusually spatulate minor wings, similar to those of 'type C'. Hrusa 16172 (Kern Co.) was thought perhaps an F<sup>1</sup> hybrid as it had relatively narrow minor wings, a smaller maximum calyx

appendage diameter, and a more condensed than usual inflorescence for 'type B', but it had a 3/3 'type B' genotype. This individual occurred where both *Salsola tragus* and 'type C' were mixed with 'type B', but a second plant of similar appearance was found mixed in a nearly pure population of 'type B' in the San Joaquin Valley north of Fresno, and it may be that this is simply an unusual 'type B' variant. The four other misclassified specimens were similar in general appearance to 'type C' yet contained only *S. tragus* haplotypes. Akers 65-1, 56-1 (Kern Co.) and 42-1, 42-3 (Stanislaus Co.) approached 'type C' in tepal-wing form, the relative persistence of mature fruit and the degree of wing development from plant base to summit, differing from 'type C' only by their slightly longer anther sacs.

TABLE 3. SEPARATION OF *SALSOLA TRAGUS* L. (TYPE A) FROM *SALSOLA 'TYPE B'*, *SALSOLA PAULSENII* LITV. AND *SALSOLA 'TYPE C'*. Numeric values are recorded maxima and minima.

Character	<i>Salsola tragus</i>	<i>Salsola 'type C'</i>	<i>Salsola 'type B'</i>	<i>Salsola paulsenii</i>
Fruit diameter incl. wing	2.9-8.4 mm $\bar{x}$ = 4.9 mm	4.6-8.1 mm $\bar{x}$ = 6.3 mm	4.8-7.9 mm $\bar{x}$ = 6.6 mm	6.6-10.7 $\bar{x}$ = 8.7 mm
Minor-wing shape	linear to blunt elliptic	narrowly obovate to spatulate	broadly obovate	obsolete or narrowly linear
Fruiting tepal	hyaline, soft, not spinose	hyaline, soft, not spinose	hyaline, soft, not spinose	sclerophyllous, spinose
Fruit/bract relationship	fruit deeply invested	fruit mostly exposed, not deeply invested	fruit exposed, not invested	fruit exposed, not invested
Winged-fruit development pattern	end of flowering season	middle of flowering season	beginning of flowering season, i.e., as individual flowers mature	end of flowering season
Winged-fruit position on stem	~upper 4/5 to 1/5 part of plant	throughout except basal two-three nodes	throughout plant	throughout plant
Tepal-wing opacity & color (fresh)	opaque, white to pink/red	opaque, white to light pink	opaque to semi-translucent, white to light pink	translucent, clear to rarely white
Tepal-wing summit margin	markedly irregular to rarely smooth	slightly irregular	smooth to slightly irregular	smooth, to slightly irregular
Anther length	0.6-1.3 mm $\bar{x}$ = 1.02 mm	0.5-1.3 mm $\bar{x}$ = 0.96 mm	0.45-0.7 mm $\bar{x}$ = 0.58 mm	0.43-0.68 mm $\bar{x}$ = 0.59 mm
Stem vestiture	sparsely to densely hispid with trichomes $>$ 0.2 mm, or +/- glabrous	sparsely hispid to +/- glabrous	glabrous or with trichomes $<$ 0.2 mm. Rarely hispid with longer trichomes	papillate
Stem vestiture position (when present)	mostly stem ribs	mostly stem ribs	stem ribs	stem rib and inter-rib area
Fruiting internode length	shorter than adjacent bract	shorter to longer than adjacent bract	gen. longer than adjacent bract	shorter than adjacent bract
Mature fruit behavior	persistent on plant	semi-persistent	abscises at maturity	abscises at maturity
Plant lifespan	annual	annual	annual to short-lived perennial	annual
Plant shape	regular, gen. wider than tall	regular to irregular, gen. open, +/- as wide as tall.	regular to irregular, taller than wide	irregular, taller than wide
Post-senescent behavior	tumbleweed	some tumbling to +/- persistent in place	+/- persistent in place	+/- persistent in place



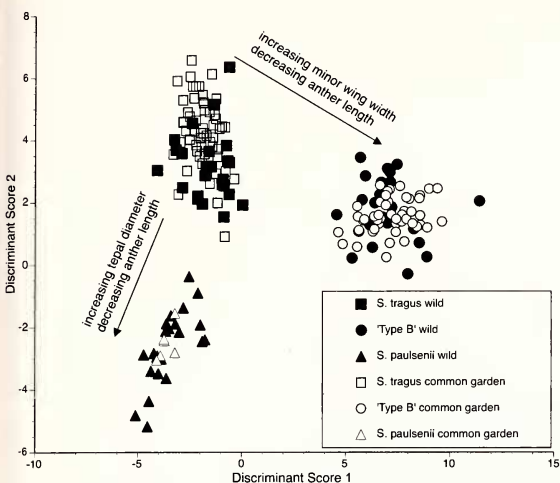


FIG. 4. Plotted discriminant scores for three characters—calyx appendage width, anther length, and minor wing width for the three 'core' groups—*Salsola tragus*, *S.* 'type B' and *S. paulsenii*. The common garden and wild-collected specimens are completely juxtaposed, evidence that there is little environmental influence on the outward form of the characteristics used for discrimination. Directional variation in the discriminant characters are labeled with arrows.

*Akers 65-1* contained three *S. tragus* haplotypes and is at least hexaploid. It is not known if *Akers 56-1*, *42-1* or *42-3* are also hexaploid or higher. *Akers 42-1* and *42-3* from Stanislaus

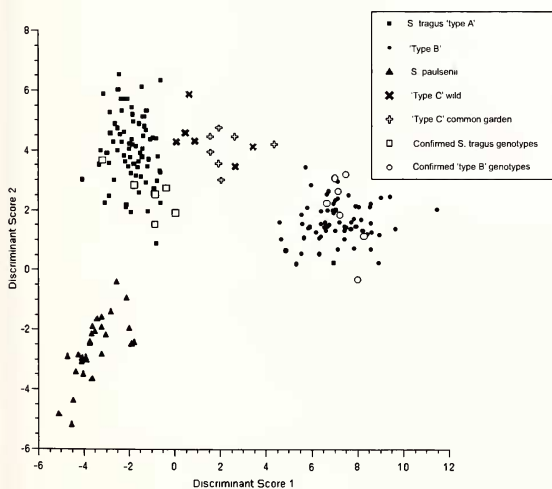


FIG. 5. Four-group discrimination plot for the Fig. 4 'core' groups plus 'type C'. Scores are based on four characters—the three Fig. 4 characters plus major-wing width. The 'type C' specimens were of known haplotype, and 'type C' from the common-garden is displayed separately from wild 'type C'. Confirmed genotypes are plotted separately from specimens identified morphologically; these are juxtaposed completely, indicating the accuracy of the morphological discrimination. Discriminant classification was 100% accurate with these morphological characters.

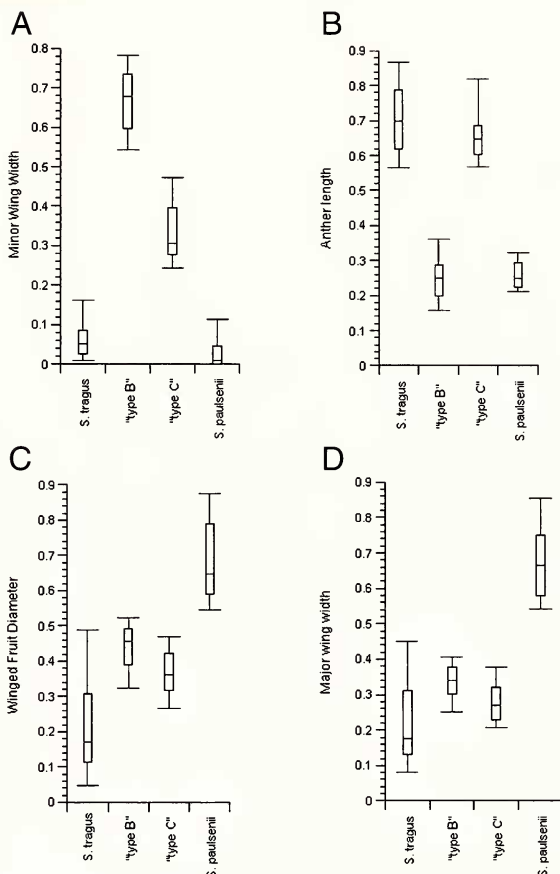


FIG. 6. Univariate comparisons among the four features discriminating California *Salsola tragus*, *S.* 'type B', *S.* 'type C' and *S. paulsenii*. Cross bar within boxes represents the mean; boxes equal one standard deviation from the mean; T-bars indicate the range. Actual sizes are scaled to between 0 and 1 using Gower's ranging algorithm (Sneath & Sokal 1973).

County in the northern San Joaquin Valley, were found isolated from the other known 'type C' populations, and *Akers 65-1* was collected in the far western Mojave Desert, an area where neither 'type B' nor 'type C' are established. Similar specimens have been seen from Washington State and the Modoc Plateau. That this is a recurring form could support the hypothesis that it represents an unrecognized polyploid. Plants of 'type C' morphology (of any genotype) appear to be relatively rare and, with the exception of the first known collection, have been found only when looked for specifically. While *Salsola tragus* is readily separable by eye from 'type B', morphologically separating this putative hexaploid form of *S. tragus* from the similar 'type C' is generally unreliable.

Quantitatively 'type B' is recognizable by its combination of laterally expanded minor wings and short anthers ( $\pm 0.5$  mm) (Fig. 4; Table 1). Its winged fruits are not invested behind the

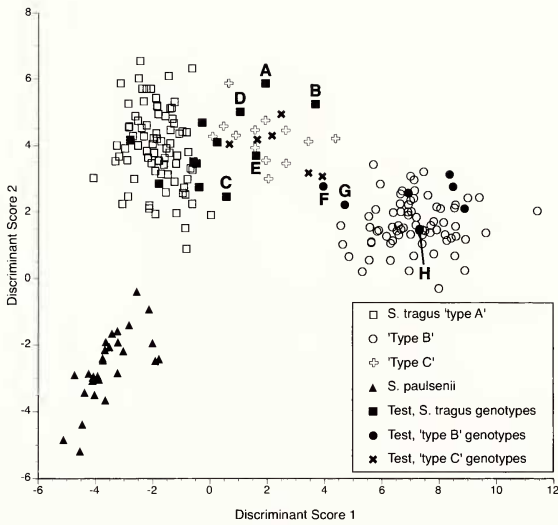


FIG. 7. Plot of scores for 25 test specimens of known genotype using the four discriminant characters in Fig. 6. Specimens classifying morphologically outside their genotype group are labeled as follows: A) *Akers 43-3*, genotype 1/2 ('type A'). B) *Akers 42-1*, genotype 2/5 ('type A'). C) *Akers 56-1* genotype 2/5 ('type A'). D) *Akers 65-1*, genotype 1/2/5 ('type A'). E) R. Moran 21152, genotype 1/2 ('type A'). F) *Hrusa 16172* genotype 3/3 ('type B'). G) *M. Rejmanek SA1*, Republic of South Africa, genotype 3/3 ('type B'). H) *C. Borger 01*, Australia, genotype 3/3 ('type B'). Collection details in Appendix III.

subtending bract, and they are non-persistent. The stem vestiture usually appears glabrous, but at higher magnification, (+/-60X), the stem ribs may have sparse and nearly microscopic (<0.2 mm) epidermal trichomes that are absent from the inter-rib areas (Fig. 9B). Trichomes like these are not known in *S. tragus*, *S. paulsenii* or 'type C'. 'Type B' is also unique within *Salsola* sect. *Kali* in that individuals sometimes overwinter and resprout the following spring. These plants do not, or rarely, grow into full size individuals, but their capacity to live past a single season is unique in *Salsola* sect. *Kali*.

Among 'type B' with 3/3 or 4/4 genotype there were no morphological correlations to either combination. However, our sample of 'type B' with known genotype is not large, and corresponding physical or behavioral patterns may not yet be visible.

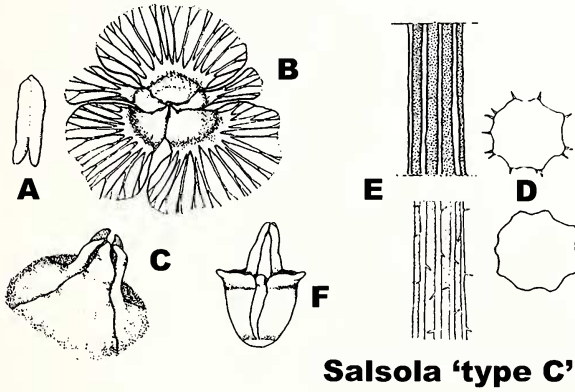
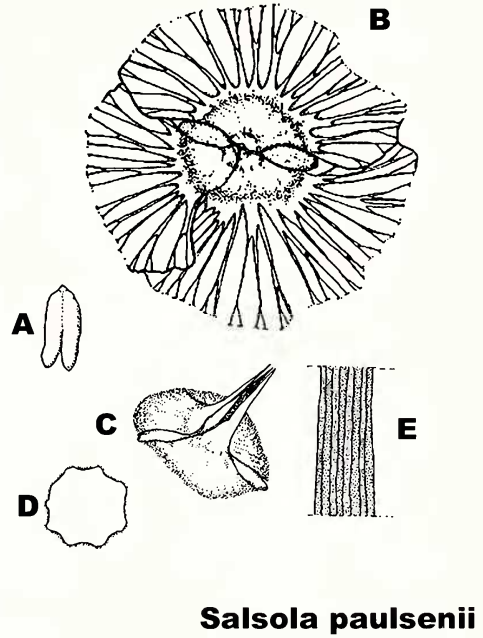
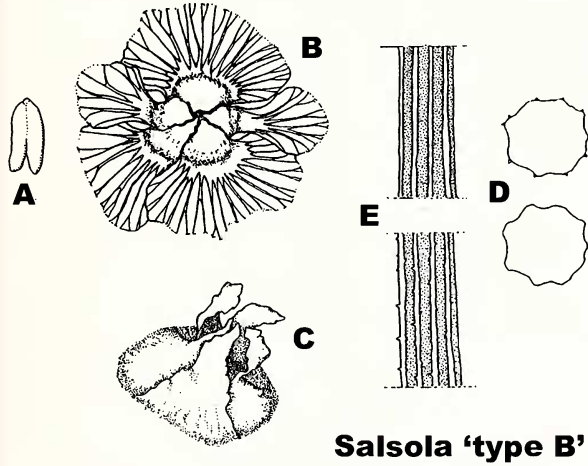
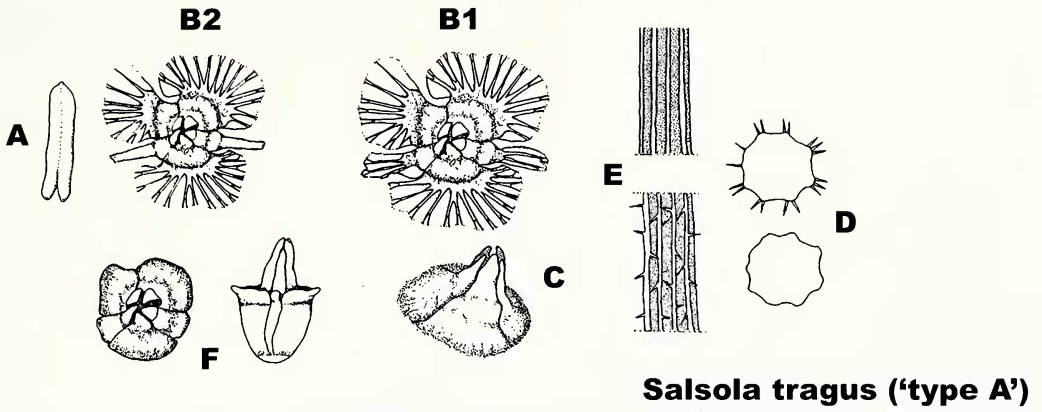
Short anthers as in 'type B' are also found in *Salsola paulsenii* (see Figs. 6B and 8), but that species combines reduced or obsolete minor wings with a broader overall winged-fruit diameter and a stem epidermal covering of dense, short, +/- columnar papillae on both the stem ribs and inter-rib areas (compare Fig. 9B and 9D). Its variability centers on the minor wings; these may be both obsolete, one may develop a narrowly oblanceolate wing, or rarely both may

be so developed. Its most prominent identifying feature is the sharp spine which, at maturity, develops from the perianth tips (Fig. 8).

Among these russiaanthistles, *Salsola tragus* is the most polymorphic. It has anthers often twice the length of those in 'type B' or *S. paulsenii* (Table 3; Figs. 6 and 8); it has reduced, but not obsolete, minor tepal-wings and a stem rib vestiture of long trichomes (Figs. 8, 9A), or none at all. Individuals may have fruiting tepal-wings similar in diameter to those of 'type B' or be half that size, produce fully winged fruits at all but the lowermost nodes, have them only at the uppermost nodes, or show a continuous enlargement of the wings from stem base to summit. Its tepal-wing margins are generally irregular and the major wing commonly has a notched tip. Wingless fruits are obscured by the subtending bract, and winged fruits are closely appressed beneath the bract and against the stem rachis. All are persistent after maturity.

As to variation among *S. tragus* in California, one is a coarse-textured, short-statured, dense, stiff, spiny and rounded tumbleweed with broad calyx wings present on fruits at nodes well down the stems; the winged-fruits are invested within the bracts and are not exposed as in 'type B'. The lowermost fruits are consistently wingless. This is the dominant form in the high and low deserts and mountainous areas. It is not generally sympatric with 'type B'. The second form is a low-elevation, late-fruiting, relatively leafy plant with small and irregular calyx-wings formed only on the top 1/5 or less of the stems; sometimes there are no winged fruits formed at all. It is common in the low elevation Central Valley, and is scattered in the Salinas Valley and South Coast region. In all these areas, it may be sympatric with 'type B'. These distinctive and common extremes probably represent part of what is actually continuous variation in a variable species. The winged fruits of these two types are compared in Fig. 8.

Characterization of *Salsola tragus* sensu stricto is further complicated by the presence of plants that bridge essentially the entire morphological gap between *S. tragus* and *Salsola paulsenii*. This intermediate is mostly in transmontane regions, and is rather common in both the field and herbarium, where specimens are identified equally frequently as *S. tragus* or *S. paulsenii*. It is found throughout the intermountain west, the Sonoran and Mojave deserts, and has a disjunct occurrence in the southern San Joaquin Valley, centering in the disturbed areas about the oil fields near Taft (Kern Co., CA). Their intermediacy is most apparent in the usual presence of stem papillae combined with a non-spinose or 'lax' mature perianth (see Mosyakin 2003), similar to *S. tragus* or 'type B'. The fruit wing texture is variable, but commonly approaches the



**SCALE**  
**A** — 0.5 mm  
**B** — 5 mm

FIG. 8. Tepal-wing, mature tepals, anther, and stem vestiture comparisons among *Salsola tragus*, *S.* 'type B', *S.* 'type C' and *S. paulsenii*. Anthers (A) and overall tepal-wing diameter (B) are scaled to facilitate comparison. A: mature anther. B: winged fruit from above. C: perianth form at fruit maturity. D: cross-section of stem showing approximate trichome size and position. E: side view of stem surface. F: lower node un-winged mature fruit in *Salsola tragus* and *Salsola* 'type C'.

hyaline form found in *S. paulsenii*. Sometimes longer trichomes, like those in *Salsola tragus* and absent from *S. paulsenii*, are mixed with the papillae typical of *S. paulsenii*, while less frequently these papillae are absent and the *S. tragus* type trichome is exclusively present. Their growth

habit is also more like the conical form of *S. paulsenii* than the rounded form of *S. tragus*. Mosyakin (2003) considered them a match to *Salsola gobicola* Iljin from central Asia and similar plants hypothesized as derived from hybridization between *S. tragus* and *S. paulsenii*

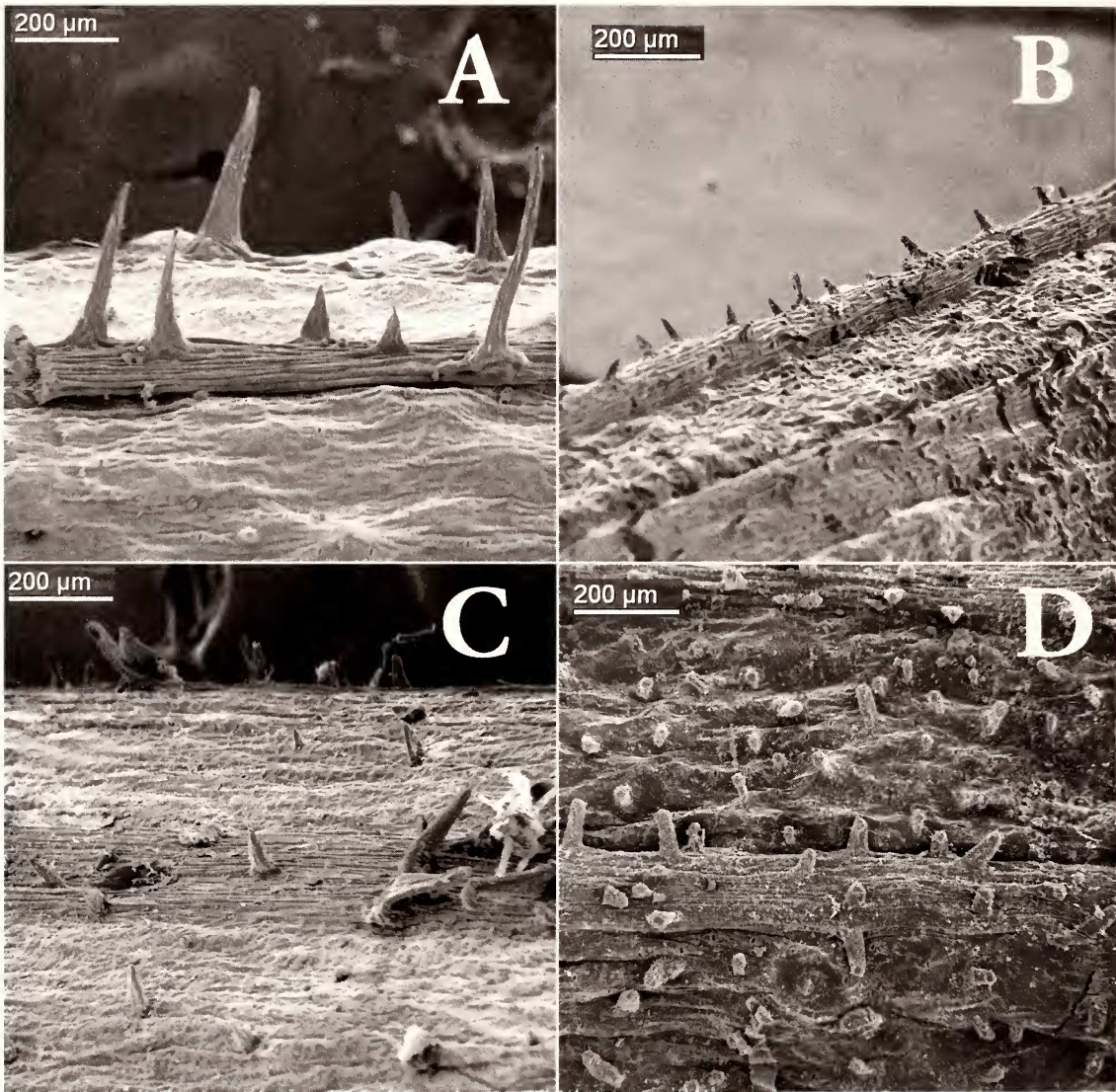


FIG. 9. *Salsola tragus*, *S. paulsenii*, *S.* 'type B' and *S.* 'type C' stem trichomes. A: *Salsola tragus*. B: *Salsola* 'type B'. C: *Salsola* 'type C'. D: *Salsola paulsenii*. Trichome density varies considerably among and within individuals. For illustration clarity trichome density displayed in *Salsola* 'type B' is greater than is typical; the remainder are representative.

are known from throughout their contact zone in that region (Rilke 1999). Its ploidy level (or levels) in North America is not known, nor is it known if this form is autochthonous here, in full or in part.

#### The Identity of 'Type B'

Among the types and regular specimens examined and photographed by S. L. Mosyakin at LE, several appeared superficially similar to 'type B'; examination of the digital images indicated that all of these were forms of *S. tragus* sensu stricto, usually plants with slightly broader than typical minor wings. Mosyakin examined

specimens from central Asia, southeast Middle Asia, Tajikistan, Kyrgyzstan, and SW Kazakhstan, but none matched 'type B'. Material at MPU from southern Europe was likewise referable to either *S. kali* sensu stricto, or *S. tragus* sensu stricto as were all host plant biocontrol vouchers from Europe, Asia and North Africa held by USDA in Albany, CA or deposited at CDA. Only Australian and South African specimens photographed at K or observed at the University of California Herbarium (UC) matched 'type B' closely. 'Type B' was comparable to the holotype image of *Salsola kali* subsp. *austroriparica* from South Africa at Munich (M), and the BM lectotype of *S. australis* also matched

'type B' closely. It was clear that both represent *Salsola* 'type B', matching in all visible characteristics, particularly the broad minor tepal-wings and the exposed winged fruits present at both upper and lower nodes. The *Salsola australis* lectotype had also short anthers and a sparse, near microscopic, vestiture like 'type B' (Table 3, Figs. 8 and 9), but these latter characters could not be seen on the image of *S. kali* subsp. *austroriparica*. Specimens at K indicated that *S. australis* is widespread in southern Australia. Our sequencing of two distinctive *Salsola* forms from that region (*C. Berger 03, 18 and 05 PERTH*) revealed both were genotype 3/3 ('type B').

Thus, there are two distinct *Salsola* species in California to which *Salsola tragus* L. has been applied; genuine *Salsola tragus* L. and *Salsola australis* R. Br. *Salsola australis* ('type B') was reported in Gaskin et al. (2006) as *S. kali* L. subsp. *austroriparica* Aellen but that report was produced before the type of *S. australis* had been seen. *Salsola australis* R. Br. has nomenclatural priority (Prodromus Florae Novae Hollandiae 411. 1810) and therefore *S. kali* L. subsp. *austroriparica* Aellen (Mitteilungen der Botanischen Staatssammlung Munchen 4. 1961) is a taxonomic synonym.

#### *Salsola australis*

California distribution.—*Salsola australis* is found throughout the San Joaquin Valley, the South Coast Ranges, the south coast, all the Channel Islands, and is apparently localized in the Colorado Desert. These areas all have warm winters without regular hard frost. Ryan and Ayres (2000) cited unspecified specimens at The California Academy of Sciences Herbarium (CAS) documenting *S. australis* in the intermountain region, but they apparently mistook intermediates between *S. tragus* and *S. paulsenii* (= *S. gobicola*) for *S. australis*. Both *S. australis* and *S. gobicola* have fruits with wings at some or all lower nodes, but as discussed previously, differ in other characteristics.

In the southern Sacramento Valley *Salsola australis* may be near the northern margin of its potential range, and populations there appear ephemeral. It is scattered along highways from about the latitude of Monterey southwards, with largest contiguous populations in the interior South Coast Ranges from southern Monterey to San Luis Obispo Cos. North of Santa Barbara, *Salsola australis*, like *S. tragus*, appears absent from the immediate coast. Southward, *S. australis* occurs right up to the intertidal zone. *Salsola australis* plants on Santa Catalina and the northern Channel Islands are similar to mainland plants, while collections from San Nicolas and San Clemente Islands are distinctive in appearance. The latter are more succulent, densely leafy and have smaller and fewer winged-fruits that are

hidden within the fleshy leaves and thus possibly not so readily dispersed than are those of the mainland forms. Although the voucher specimen has not been found, the report by Mosyakin (1996, and cited in Hrusa et al. 2002) of *S. kali* subsp. *pontica* (Pall.) Mosyakin on San Nicholas Island is probably also this form of *S. australis*.

Among the mainland populations, there were two minor, more or less allopatric morphs of *Salsola australis*. Plants from the South Coast Ranges were semi-succulent, irregular in habit, brittle, often blue-glaucous in color, and tended to have smaller winged-fruit diameter than did plants from the San Joaquin Valley and south coastal region, although not so small as those on San Nicolas and San Clemente Islands. Uncorrelated to these two morphs was a minor bimodal distribution of the minor-wing width that was also geographically uncorrelated.

Distribution outside of California.—As far as currently known, in western North America outside of California, herbarium specimens of *Salsola australis* have been seen from Arizona, southwestern Texas and low elevations in Mexico. A survey of specimens from the remainder of North America has not been undertaken, and, given the confusion with *S. tragus*, it is clear that its non-California North American distribution is scarcely known.

Outside of North America, we have seen specimens from Australia, Namibia and the Republic of South Africa. Because species of *Salsola* sect. *Kali* have been thought indigenous only to the northern hemisphere (Mosyakin 1996; Rilke 1999), its presence in the southern hemisphere was assumed adventive (Botschantzev 1974; S. L. Mosyakin, Kholodny Institute of Botany, Kiev, Ukraine, personal communication). This led to the interpretation that *S. australis* was a form of Eurasian *S. tragus*. Examination and molecular evaluation of additional Australian and southern Africa *Salsola* materials would be useful, both to confirm the presence or absence of *Salsola tragus* sensu stricto in those regions, but also to elucidate the diversity of *S. australis* genotypes there. Our limited sampling revealed only haplotype 3 in African and Australian *S. australis*. However, if the taxon had a long association with one or more of those regions additional haplotypes would be expected, including haplotype 4, common in North American *S. australis*, but not yet found elsewhere. Australian specimens at K appear to represent both morphological forms of *S. australis* found in California. The lectotype compared most favorably with succulent material from the California inner South Coast Ranges, while the holotype of *S. kali* subsp. *austroriparica* is apparently more like the San Joaquin, South Coast, and Arizona forms. In addition, two Australian specimens (*C.*

*Borger 06, 18 PERTH*) of what has been called *S. australis* var. *strobilifera* (Benth.) Domin, a plant distinct from *S. australis sensu stricto* in its densely congested 'strobilus'-like inflorescences, but with similar tepal-wings, had genotype 3/3. A third Australian form (*C. Borger 05 PERTH*), was a prostrate sand dune plant, similar in habit to *S. kali* from European and North African coastal sands. This genotype 3/3 plant has calyx wings similar to *S. australis* in form and texture, but with narrower minor-wings. It is of note that in Flora of Australia (Wilson 1984) the '*Salsola kali*' illustrated is *S. australis*, which is listed as a synonym, while *S. tragus* is not mentioned nor listed in the synonymy. Our untested hypothesis is that *Salsola* sect. *Kali* of Australia represents a disjunct species complex and *S. australis* as treated here is just the typical form.

Habitat differences.—*Salsola australis* occurs in California from sea level to about 400 m, and reaches at least 500 m in Arizona. Contrary to *Salsola tragus*, which is common in the Mojave Desert, *S. australis* is there only a rare casual. It has recently been collected in the low warm desert of California near the Mexican border (*R. Riefner 07-64 CDA*), and the few specimens so far seen from Mexico were also collected at low elevations. Above about 400 m in California *Salsola tragus* replaces *S. australis*; in general *Salsola tragus*' adaptation seems to favor more severe environments and its widespread occupation of interior North America (see Mosyakin 2003) is further evidence.

Distribution (and often morphological) patterns within or among widespread indigenous taxa commonly correspond to some ecologic or geographic condition, while widespread adventive plants rarely display such coherence, occupying more or less disturbed areas in many types of habitat. Their distributions often reflect better the relatively random movement of specific, usually human, vectors. *Salsola tragus* and *Salsola australis* overlap in range and are often sympatric at low elevations, but when growing adjacent they generally occupy different habitats. For example, in favorable years on the open shale hills of the South Coast Ranges east of San Lucas in Monterey Co., *Salsola australis* occupies thousands of acres with *S. tragus* restricted to patches along valley bottom fences and immediate roadsides.

Some of the microhabitat separation may be the result of different dispersal mechanics. The fruits of *S. tragus* are invested by the subtending bract, tightly appressed to the rachis and persistent after maturity. The mature fruits do not abscise readily and are dispersed as the plant tumbles, or as it decomposes post-tumbling. This pattern has been documented for *Salsola tragus* (reported as *S. iberica*) in the Great Basin

(Stallings et al. 1995). Conversely, the fruits of *Salsola australis* generally abscise readily at maturity (see Table 3), and the plant skeletons do not tumble to any extent. The result is that *Salsola australis* is often found on hillslopes and steep roadcuts where the parent plants grew. This dispersal behavior may also hold for Australia, where, according to C. Borger (University of Western Australia, Perth, personal communication) their 'russianthistle' does not tumble. Commonly one can also recognize the two species when pressed and dried by the accumulated pile of loose separated fruits in mature *S. australis*, something not seen with *Salsola tragus* specimens.

#### A Name for 'Type C'

All but four of the individuals morphologically referable to 'type C' had combined *S. tragus* and 'type B' haplotypes. Those four with *S. tragus* genotypes only, have been discussed above. The remaining 'type C' individuals with three different haplotypes were almost certainly hexaploid with two chromosome sets from tetraploid *S. tragus* and one from diploid 'type B'. Without additional data it could not be confirmed that the Sutter County genotype 2/3 and Coalinga genotype 1/4 plants were also hexaploid; their *Salsola tragus* parents may have been tetraploid homozygotes and thus only two distinguishable haplotypes are present in the hybrid.

In our view, genuine 'type C' is a fertile allohexaploid derived via hybridization between diploid *Salsola australis* and tetraploid *Salsola tragus*. These allohexaploid derivatives would be inter-fertile among themselves, yet inter-sterile to the parent diploids or tetraploids. At least two persisting, true-breeding populations of 'type C' are present in California and appear to represent at least a locally adapted entity. This inter-fertility among 'type C' individuals and the offspring sterility expected if a hexaploid is backcrossed to tetraploid *S. tragus* or to diploid *S. australis* supports the hypothesis that 'type C' is a biologically distinct species. It has originated at least three times, with each instance a formation of the same species.

We hereby propose the following specific epithet be applied to 'type C'.

***Salsola ryanii* G. F. Hrusa and Gaskin sp. nov.** (Fig. 8). TYPE: USA, California, Kern Co., Hwy 119, 0.5 mi W of Old River. Genotype 2/5/4, 35.267°N, 119.153°W. El. 315 ft. 01 Nov. 2002, *P. Akers 69-3* (Holotype CDA; isotypes DAV, RSA).

***Salsola ryanii* sp. nov.** Planta annua usque ad 2 m alta. Caules cylindrici, sparse hispidi vel glabri. Fasciculi collenchymatis plerumque virides, interdum rubentes. Fructuum alae tepalum

albae vel subroseae, venis visibilibus sed non prominentibus. Alae minores tepalum plus minusve spathulatae, infra angustatae supra expansae, limbo ungue latiore. Fructus, alis inclusis, 5.3–7.2 mm in diametro. Fructus superiores alati, basales partim alati vel non alati. Tepala in maturitate hyalina remanentia, mollia. Fructus in maturitate semipersistens, bractea subtendenti partim investitus. Antherae 0.5–1.3 mm longae.

*Annual* plant up to 2 m tall. *Stems* cylindric, sparsely hispid or glabrous. *Stem ribs* usually green, sometimes reddening. *Tepals* in maturity remaining hyaline, soft. *Wings of tepals* of fruits white or pinkish, with veins visible but not prominent. *Minor-wings* of tepals more or less spatulate, below narrowed, above expanded, with limb broader than claw. *Fruit*, wings included, 5.2–7.2 mm in diameter; upper fruits winged, basal partly winged or not winged. At maturity semipersistent, partly invested by subtending bract. *Anthers* 0.5–1.3 mm long.

The epithet honors Fred Ryan of the USDA/ARS, who first collected and recognized this entity.

*Visual recognition* *Salsola ryanii*. Figures 8 and 9 illustrate tepal-wing, anther, and stem vestiture morphologies and Table 3 compares taxonomically useful morphological traits of *S. ryanii* ('type C'), *S. australis*, *S. paulsenii* and *S. tragus*. *Salsola ryanii* is morphologically intermediate between *S. tragus* and *S. australis* in nearly all features, and this intermediacy makes it a challenge to recognize on its own. Adding to the difficulty are those few *S. tragus* plants that are similar morphologically to *S. ryanii*. The general texture of 'type C' is difficult to assess on a dried herbarium sheet; it is a thinner-stemmed and less brittle plant than the often thick-stemmed and semi-succulent *S. australis*, and more brittle than the wiry and tough *Salsola tragus*. It does not form the long, dense, spiciform inflorescence common in mature *Salsola tragus*, nor does it have the loose, more or less uncondensed inflorescence of most *Salsola australis*. When growing side by side with *S. tragus*, *Salsola ryanii* may be distinguished by the relatively long internodes and winged fruits at lower nodes. Identification is improved by becoming familiar with the parents. Distinguishing genuine 'type C' plants from hexaploid *S. tragus* failed using our discriminant characters, as discussed previously. The latter are apparently less hispid and more robust than *S. ryanii*, but further study will be necessary before these can be reliably separated using morphology alone. However, they are readily distinguished using molecular markers.

*Distribution.* *Salsola ryanii* is known from three localized small to extended medium-sized popu-

lations (Fig. 3A). All occur below 300 m and occur where *Salsola australis* and *Salsola tragus* are sympatric. Two populations are along regional highways; at the intersection of Hwy. 166 and Hwy. 33 near Maricopa (Kern Co.) and alongside Hwy. 33 immediately north and south of Coalinga (Fresno Co.). In both locations *Salsola ryanii* grows mixed with *Salsola tragus*. The largest populations are along Highways 166 and 119 from immediately east of Maricopa east to Bakersfield (Kern Co.). It has also been collected near Famoso and Shafter in that region. The area from south of the Fresno Co. line, north of Hwy. 166, east of the Elk Hills and west of approximately Interstate 5 has scattered small to medium-sized patches of *S. ryanii*. In this region, it is sympatric with *S. tragus*, *S. australis* and sometimes *S. gobicola*, although the two latter are often growing on sands or shales while *Salsola ryanii* is usually on the deeper soils *S. tragus* occupies. The two small populations in Sutter County have not been relocated, and as with the *S. australis* in that area, may be ephemeral. The haplotype combinations in *Salsola ryanii* are geographically localized and point to regional dispersal from either a local origin or introduction; as all these sites are along or close by roadsides, it is conceptually easy see their dispersal as predominantly human-mediated.

*Will it spread?* Most novel hybrids are not selectively advantageous, but evidence is growing that hybrids or novel genotypes are involved in many invasions (Ellstrand and Schierenbeck 2000). Infamous recent examples include the marsh grass *Spartina* spp. (Ayles et al. 1999), the freshwater aquatic plant *Myriophyllum* spp. (Moody and Les 2002), saltcedar shrubs (*Tamarix* spp.) (Gaskin and Schaal 2002), the marine alga *Caulerpa* spp. (Durand et al. 2002), and a mustard (*Rorippa* spp.) (Bleeker 2003). In addition to potentially stimulating invasiveness, novel hybrids also may affect control efforts by presenting phenotypes that are novel to potential classical biological control agents. Analysis of invasion identities and population dynamics using genetic markers has contributed much information about species that are biological control targets (Sakai et al. 2001; Roderick and Navajas 2003).

Abbott (1992) summarized four known allopolyploid speciation instances, two between pairs of non-native taxa and two between native and non-native taxa. Both instances of non-natives crossing with other introductions are in North America; two species of *Tragopogon*, *T. dubius* and *T. pratensis*, have given rise to *Tragopogon miscellus* Ownbey (Amer. J. Bot. 37: 498. 1950) that has spread beyond the range of one parent. The other, *T. mirus* Ownbey (Amer. J. Bot. 37: 498. 1950), a product of hybridization between *T.*

*dubius* and *T. pratensis*, has not spread beyond the vicinity of its parent species. In Great Britain, *Senecio cambrensis* Rosser (Watsonia 3: 228, 1955) has been derived at least twice between the native *Senecio squalidus* and introduced *Senecio vulgaris*, and is always found where both parents are present. *Salsola ryanii* appears to behave similarly to the *Tragopogon mirus* and *Senecio* models; it has originated at least three times, but each known independent derivative remains in the region of the parent species. In this case, although *Salsola* sect. *Kali* travels readily in concert with humans and the current populations of *Salsola ryanii* may be distant from their sites of origin, they still occur within the parents adaptive range. *Salsola ryanii* may be restricted in distribution at least in part due to its intermediacy in the differing ecological adaptations characterizing the parents; fruits do not abscise readily, nor are they persistent; plants tumble to some small extent, but are not dense and orbicular like *S. tragus*. We feel, based on its current distribution pattern of isolated or extended roadside patches that *S. ryanii* will likely spread only locally by non-anthropogenic means, but will attain longer distance dispersal via human traffic. Its present adaptive deficiencies will, to some extent, probably restrict its subsequent movement, and the species will unlikely become a widespread future pest.

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- inds. 1–6; row B-6/inds. 1–5; row C-5/inds. 1–6; MERCED CO.: Santa Nella, water tower on Hwy 33, 37°4.3'N, 121°1.2'W, Row B-2/inds. 1–5; row A-4/inds. 1–8. SAN DIEGO CO.: Mission Valley, Hazards Center Dr. off I-8. 32° 46.1'N, 117°9.2'W, Nov. 1999. Row A-5/inds. 1–7; row C-4/ inds. 1–6; row B-7/inds. 1–6.*

#### *Salsola tragus* ('type A')

USA: CALIFORNIA: FRESNO CO.: Fresno, 30 acre field adjacent to HCRL RR, 36°43.3'N, 119°44.1'W, Nov. 1999. *Row A-1/inds. 1–4; row B-5/ inds. 1–6; row C-10/inds. 1–4; Big Field in Fresno, 36°48.9'N, 119°44.1'W, Dec. 1999; row A-3/inds. 1–6; row B-1/inds. 1–4; row C-1/inds. 1–5; Coalinga, Phelps Rd. at Hwy 33, 36°9.9'N, 120°21.2'W, row B-4/inds. 2–4; row C-6/inds. 1–4; row A-9/inds. 1, 3, 4. YOLO CO.: Davis, Koso St. at Cowell Blvd. 38°32.1'N, 121°44.1'W, Dec. 1999. *Row A-8/inds. 1–6; row C-3/ inds. 1–5; row B-9/inds. 1–4.**

#### *Salsola paulsenii*

USA: CALIFORNIA: SAN BERNARDINO CO.: Barstow, downtown Business I-15 and E. White St. 34°54'01"N; 117°01'22"W, 650 m, *row B-8/inds. 1–3; row A-2/inds. 1–2; row C-9/1 ind.*

#### *Salsola* 'type C'

USA: CALIFORNIA: FRESNO CO.: Coalinga, Phelps Rd. at Hwy 33, 36°9.9'N, 120°21.2'W, *row C-2/inds. 2, 3; row A-10/inds. 2, 3; row B-3/inds. 1, 3, 4.*

### Wild Materials

#### *Salsola* 'type B'

USA: CALIFORNIA: FRESNO CO.: *Fuller 18732 S* side Hwy 149 (Hwy 198) 2.1 mi. W of Coalinga. 7/24/1969. IMPERIAL CO.: *R.E. Reifner 07-64*, disturbed alkaline flats on Ross Rd. ca. 0.2 mi. E of Dogwood St. N. of Hwy 8, nr. El Centro. UTM: (NAD 83) 11S 063755E, 362805 N. El. minus 28 ft. 02/17/2007. KERN CO.: *Hrusa 16169*, 1/4 mi. W of Maricopa on Hwy 166/33, 35.056°N, 119.405°W, 925 ft. el. 10/12/2003. *Hrusa 16173* Hwy 166/33 10 mi. E of Maricopa. 35.058°N, 119.258°W, 600 ft. el. 10/12/2003. *H.L. Green s.n.*, near Buena Vista Lake, 11/10/61. KINGS CO.: *Fuller 12935* E slope Pyramid Hills, 14 mi. S of Avenal. 12/17/1964. LOS ANGELES CO. *B. Villegas B247-3; B247-4; B247-5*, all haplotype 4. Plant DNA#s in Gaskin et al. 2006. Calabasas nr. Ventura Co. line. 34°9.93'N. 118°40.67', 8/21/2002; *M. O'Brien s.n.* Figueroa Blvd., Los Angeles. 9/13/2004. *M. O'Brien s.n.* Pescadero State Beach. 12/23/2004. MONTEREY CO.: *Hrusa 16182* RR tracks at Monterey Rd. on E side US 101 (Rancho del Salinas). 36.675°N, 120.694°W. 683 ft. el. 10/14/2003. *Hrusa 16183A*. Plant DNA# in Gaskin et al. 2006; *16183B; 16183C; 16183D*. Plant DNA#s in Gaskin et al. 2006. All haplotype 3. Hwy 198 betw. San Lucas & Coalinga +/- 1 mi. E US 101. 36.149°N. 121.002°W. 492 ft. el. 10/14/2003. *Hrusa 16188*. Gonzales, W side US 101 at corner Folletta & Atta Rds. 36.524°N, 121.466°W, 100 ft. el. 10/14/2003. *Hrusa 16193*, haplotype 3. Plant DNA# in Gaskin et al. 2006. Jolon Rd. at Lockwood Post Office. 35.937°N, 121.072°W, 970 ft. el. 10/14/2003. SAN BENITO CO.: *Hrusa 16186*. Hwy 25, S of Paicines, vineyard edge. 36.677°N, 121.256°W, 782 ft. el. 10/14/2003. SAN JOAQUIN CO.: *Hrusa 16134* Hwy 33 exit 1/2 mi. S of Interstate 5. 37.672°N, 121.333°W.

### APPENDIX I

Specimens used in the morphometric analysis. Some of these are also cited in Gaskin et al. (2006). Specimens with genotypes determined specifically for this study are also listed in Appendix II. "Common garden" collection data are seed collection provenances; vouchers for the original parent material are not available. Offspring vouchers are at CDA except where specified.

### Common Garden Materials

#### *Salsola* 'type B'

USA: CALIFORNIA: FRESNO CO.: Fresno, HCRL RR tracks, 36°43.3'N, 119°44.1'W, *Row A-6/*

75 ft. el. 10/10/2003. SAN LUIS OBISPO CO.: *Hrusa 16179*, Cuyama Cyn. along Hwy 166 betw. Cuyama & Santa Maria. 35.047°N, 120.183°W, 896 ft. el. 10/13/2003. *Hrusa 16181*, Templeton, US 101 1/4 mi. N of Paso Robles Ck. Bridge. 35.536°N, 120.711°W, 775 ft. el. 10/13/2003. *Hrusa 16196*, Hwy 46 E of Paso Robles, immed. E of Whitley Gardens. 35.659°N, 120.480°W 1050 ft. el. 10/14/2003.

*Salsola tragus* ('type A')

USA: CALIFORNIA: INYO CO: *Hrusa 16709 C DFA IPC seed accession RT05-3; 16710*; Hwy 6 roadside, 6 mi. N of Bishop, 37°24'49"N, 118°21'11"W, 4100 ft. el. 9/27/2005. KERN CO: *Akers RT-056-3*. N of Hwy 58, int. Edison Hwy & Tower Line Rd. along RR. 35.332°N, 118.807°W, 794 ft. el. 10/30/2002. *Hrusa 16787 C DFA IPC seed accession RT05-14A* genotype 1/2. Hwy 43 S of Shafter, open silty field. 35°26'10"N, 119°15'19"W, 375 ft. el. 9/29/2005. *Hrusa 16813 C DFA IPC seed accession RT05-18*, genotype 1/2; *Hrusa 16814 C DFA IPC seed accession RT05-19*, genotype 2/5, sag pond on San Andreas fault, S end Carrizo Plain. 34°59'55"N, 119°29'19"W, 9/29/2005. LOS ANGELES CO: *O'Brien s.n.* Roadside, Gorman. 11/3/2005. MONO CO.: *Hrusa 16697* Corner of Hwy 395/Hwy 89. 38°38'55"N, 119°31'50"W, 5100 ft. el. 9/27/2005. MONTEREY CO.: *Fuller 14184* N side Hwy 198 1.5 mi. W of Coalinga. 10/7/1965. SAN LUIS OBISPO CO.: *Fuller 14179, 14180*, Hwy 466 (Hwy 46) 1.3 mi. W of Shandon. 10/7/1965. *Fuller 14181* S side Hwy 466 (Hwy 46) N of Shandon. 10/7/1965. *Hrusa 16817; 16818; 16819; 16820; 16821; 16822*, S end of Elkhorn Plain. 35°01'36"N, 119°29'27"W. 2500 ft. el. 9/29/2005. SAN BERNARDINO CO.: *Akers RT-065-3* Old AFB, Phantom West Rd. and Aviation Dr., 34.590°N, 117.366°W. 2850 ft. el. 10/31/2002. NEVADA: NYE CO.: *Hrusa 16727* genotype 2/5; Hwy 95 roadside at Esmeralda Co. line. 37°27'58"N, 117°10'07"W. 4500 ft. el. 9/27/2005. WASHOE CO.: *Hrusa 16691; 16692; 16693*; Mogul exit off Interstate 80, +/- 10 mi W of Reno. 39.517°N, 119.923°W, 4800 ft. el. 9/26/2005.

*Salsola paulsenii*

USA: CALIFORNIA: INYO Co.: *Hrusa 16736, 16737 C DFA IPC seed accession RT05-5, 16738*, Tecopa, Death Valley, Corner Old Spanish Trail Rd. & Furnace Lake Rd. on rd. to China Rch. 35°50'51"N, 116°12'08"W. 1500 ft. el. 9/27/2005. KERN CO: *Fuller 18837* S side Hwy at W limits of Boron. El. 2450 ft. 8-21-1969. SAN BERNARDINO CO.: *Fuller 12644* S side Hwy 66 to Daggett, E limits of Barstow. 9/22/1964; *Fuller 12645* Hwy. To Barstow, 2.6 mi. W of Daggett. 9/22/1964; *Fuller 15216*, disturbed ground, 2 mi. E of Barstow on I-40, 9/28/1966. *Fuller 15217*, S of I-40 to Daggett, 2 mi. E of Barstow. 9/28/1966. *Hrusa 16740 C DFA IPC seed accession RT05-7*, Dumont Dunes, Death Valley, 9/27/2005; *Hrusa 16744 C DFA IPC seed accession RT05-8, 16745 C DFA IPC seed accession RT05-9*, NE edge of Silver Lake, edge Hwy 127, 35°22'34"N, 116°07'23"W, 900 ft. el. 9/27/2005. *Hrusa 16757 C DFA IPC seed accession RT05-11, 16756, 16758, 16759*, Mojave R. bed in BLM Afton Cyn Preserve. 35°02'51"N, 116°23'54"W, 1400 ft. el. 9/28/2005. *Hrusa 16761 C DFA IPC seed accession RT05-12, 16762, 16763, 16765, 16766* Daggett, sandy bank of Mojave River. 34°52'34"N, 116°53'27"W 2000 ft. el. 9/28/2005. *Hrusa 16775 C DFA IPC seed accession RT05-13, 16776, 16777*, Hwy 58 betw. Kramer Jtn. And

Barstow on Harpur Lake Rd. at RR track crossing. 34°57'03"N, 117°19'59"W. 2700 ft. el. 9/28/2005.

*Salsola* 'type C'

USA: CALIFORNIA: KERN CO.: *Akers RT-056-2*, genotype 2/5/4, N of Hwy 58, int. Edison Hwy & Tower Line Rd. along RR. 35.332°N, 118.807°W, 794 ft. el. 10/30/2002. *Akers RT-069-3*, genotype 2/5/4, Hwy 119, 0.5 mi. W of Old River. 35.267°N, 119.153°W. 315 ft. el. 11/01/2002 (holotypus). *Akers RT-72-1*, genotype 2/5/4, *RT-072-2*, genotype 2/5/4, Elk Hill Rd., NE base of Elk Hills. 35.333°N, 119.463°W, 395 ft. el. 11/01/2002. SUTTER CO.: *Hrusa 15999*, genotype 2/3, Yuba City downtown rd. edge. 10/01/2001. YUBA CO.: *Akers RT-010-2*, genotype 2/3, *RT-10-3* genotype 2/3, Smartville Rd., 0.3 mi. N of Daugherty. 39.186°N, 121.304°W. 100 ft. el. 9/19/2002.

APPENDIX II

'Type C' specimens whose PEPC intron genotypes were determined for this study. CG = "common garden". See Appendix I for additional specimen data. The 14 specimens marked with an asterisk were confirmed 'type C' genotypes and used in the discriminant function calculations. The remainder were used in tests of those functions (Fig. 7, Table 1 and Appendix - III).

Genotype	Specimen	County	Plant DNA #
2/5/4	Akers RT-069-2	Kern	6111
2/5/4	*Akers RT-069-3	Kern	6112
2/5/4	*Akers RT-072-2	Kern	6116
2/5/4	Akers RT-055-1	Kern	6106
2/5/4	*Akers RT-072-1	Kern	6115
2/5/4	*Akers RT-056-2	Kern	6108
1/4	CG: C-2/1	Fresno	6125
1/4	*CG: C-2/2	Fresno	6126
1/4	*CG: C-2/3	Fresno	6127
1/4	CG: A-10/1	Fresno	6117
1/4	*CG: A-10/2	Fresno	6118
1/4	*CG: A-10/3	Fresno	6119
1/4	CG: A-10/4	Fresno	6120
1/4	*CG: B-3/1	Fresno	6121
1/4	CG: B-3/2	Fresno	6122
1/4	*CG: B-3/3	Fresno	6123
1/4	*CG: B-3/4	Fresno	6124
2/3	*Akers RT-010-2	Yuba	6101
2/3	*Akers RT-010-3	Yuba	6102
2/3	*Hrusa 15999	Sutter	6133

APPENDIX III

*Salsola tragus*, S. 'type B' and S. 'type C' specimens used to test the efficacy of the discriminant functions. Groupings below are based on correlation to those in Fig. 5. Vouchers at CDA unless specified. See also Table 1.

*Salsola* 'type B'

AUSTRALIA: *C. Borger 01*, genotype 3/3. Geraldton, Western Australia (PERTH). CALIFORNIA: KERN CO.: *Hrusa 16172* genotype 3/3. Hwy 166/33

\* Plant DNA#s in Appendix II.

10 mi. E of Maricopa. 35.058°N, 119.258°W. 600 ft. el. 10/12/2003; *Akers RT-074-1* genotype 3/3. E side Hwy 46/I-99 interchange. 35.601°N, 119.208°W, 415 ft. el. 11/01/2002. LOS ANGELES CO: *B. Villegas B247-1; B247-2*; genotype 4/4, Calabasas nr. Ventura Co. line. 34°9.93'N, 118°40.67', 8/21/2002. MERCED CO.: *Akers RT-030-2* genotype 4/4. Billie Wright Rd. ~0.4 mi. W of I-5 bridge. 37.04°N, 120.96°W, 246 ft. el. 10/10/2002; *Akers RT-013-1* genotype 4/4. S side Hwy 152. 36.983°N, 121.374°W, 255 ft. el. 09/23/2002; REPUBLIC OF SOUTH AFRICA: *M. Rejmanek SAI*, genotype 3/3. Kimberley region. 10/28/2005.

*Salsola tragus* ('type A')

MEXICO: BAJA CALIFORNIA: *Moran 21152* genotype 1/2. Four mi. W of Ojos Negros. 31°53'N, 116°22'W, 600 m el. 11/10/1973. UNITED STATES: CALIFORNIA: BUTTE CO.: *Ahart 8295* genotype 1/2. E side Sacramento River 1 mi. SE of Ord Ferry. 105 ft. el. 10/3/1999. FRESNO CO.: Common garden row *A-7/2-4*, all genotype 1/2. *Akers RT-014-1* genotype 2/5. Kearney Research Center, Rio Vista Rd. 0.1 mi. N

of Manning. 36.606°N, 119.473°W, 353 ft. el., 09/23/2002. KERN CO: *Akers RT-056-1* genotype 2/5. *Akers 65-1* genotype 1/2/5. Old AFB, Phantom West Rd. and Aviation Dr. 34.59°N, 117.366°W, 2850 ft. el. 10/31/2002. SOLANO CO: *Akers RT-005-3* genotype 1/2 (Gaskin et al. 2006). Corner of Robben & Hackman Rds. 38.453°N, 121.179°W. 43 ft. el. 09/18/2002. STANISLAUS CO.: *Akers RT-042-1*, genotype 2/5, *Akers RT-042-3*, genotype 1/2, Radio tower, ~6 mi. E of Turlock at Main & Central. 37.491°N, 120.957°W. 46 ft. el. 10/28/2002.

*Salsola* 'type C'

CALIFORNIA: FRESNO CO.: Common garden row *C-2/lind. 1*; row *A-10/linds. 1, 4*; row *B-3/lind. 2*, all genotype 1/4. Coalinga, Phelps Rd. at Hwy 33, 36°9.9'N, 120°21.2'W. KERN CO.: *Akers RT-055-1* genotype 2/5/4, Shafter, vacant lot to W of Santa Fe Way ~1000 ft. N of Hagemon. 35.400°N, 119.151°W. 10/30/2002. *Akers RT-069-2*, genotype 2/5/4, Hwy 119, 0.5 mi. W of Old River. 35.267°N, 119.153°W. 315 ft. el. 11/01/2002.